PREDATOR-PREY RELATIONSHIP BETWEEN PACIFIC HERRING, *CLUPEA HARENGUS PALLASI,* LARVAE AND A PREDATORY HYPERIID AMPHIPOD, *HYPEROCHE MEDUSARUM*[1]

Hein von Westernhagen and Harald Rosenthal[2]

ABSTRACT

Predatory efficiency of *Hyperoche medusarum* (Hyperiida, Amphipoda) on yolk-sac larvae of Pacific herring, *Clupea harengus pallasi*, was studied in the laboratory under continuous light conditions: 1, 5, 10, and 50 herring larvae were exposed to 1, 2, 4, 8, and 16 hyperiids in 500-ml beakers. It was found that the number of attacked larvae per unit time increased with rising predatory and/or prey density. Individual mean predation rate was found to decline with increasing predator as well as prey densities, prolonged exposure times, and the presence of alternative prey.

Aside from starvation (Sette 1943; Schnack 1972), one major cause of mortality in marine fish larvae is assumed to be predation (Stevenson 1962), the predators frequently being crustaceans, as described by Garstang (1900), Lebour (1925), Davis (1959), Lillelund (1967), Rosenthal (1967), Kabata (1970), Lillelund and Lasker (1971), Theilacker and Lasker (1974), and others. The pelagic hyperiid amphipod *Hyperoche medusarum* occurs commonly off the Oregon coast (Lorz and Pearcy 1975), in Californian waters (Hurley 1956), in the North Atlantic (Shoemaker 1930; Bowman et al. 1963; Dunbar 1963), in the North Sea (Sars 1895; Evans and Sheader 1972), and in New Zealand waters (Hurley 1955). In British Columbia waters it occurs commonly in the upper layers (<30 m) of the water column (Bowman 1953), and in Departure Bay (Vancouver Island) its juveniles are frequently found clinging to the exumbrellae of hydromedusae (Westernhagen 1976).

The cooccurrence of large numbers of juvenile *H. medusarum* with newly hatched larvae of the Pacific herring, *Clupea harengus pallasi*, was incidentally discovered in 1974 at the pier of the Pacific Biological Station, Departure Bay. Field observations indicated that *Hyperoche* juveniles preyed on herring larvae and occasionally on other fish larvae. Since this was the first record on a possible predator-prey relationship between *H.* *medusarum* and marine fish larvae, this study was initiated to shed some light on the predatory efficiency of this amphipod.

MATERIAL AND METHODS

For prey, yolk-sac larvae (8.0-9.5 mm TL (total length)) of the Pacific herring incubated in the laboratory were used. Immature *H. medusarum* (1.48-1.80 mm TL) which had aggregated beneath a light at night were caught with a pail and separated from other plankton organisms with a large bore pipette.

Experiments were performed in filtered seawater in 500-ml beakers (salinity 28‰; temperature 9°C; constant light). The water surface of the beakers was covered with 300-μm mesh size nylon gauze in order to keep the amphipods from breaking through the surface. Because *Hyperoche* specimens in their natural habitat were occasionally found resting on the exumbrellae of medusae, a strip of nylon gauze (50 × 20 mm) hanging from the surface cover provided attachment for the amphipods when needed.

Different numbers of herring larvae 1, 5, 10, and 50 were exposed to 1, 2, 4, 8, and 16 hyperiids for three exposure periods (2, 4, and 8 h). The number of replicates for all predator/prey ratios were 4, 6, and 5 for the 2-, 4-, and 8-h exposure periods. Some additional experiments with 6- and 10-h exposure periods were used for the computation of a mean attack rate on the basis of 111 h of observation. Eleven trials using 25 herring and 25 flatfish larvae with 16 amphipods were also conducted. One additional control vessel (50 herring larvae, no

amphipods) was used for each exposure period. Mortality of larvae was measured every 2, 4, and 8 h by means of direct counts. All remaining larvae were removed, and healthy, wounded, and dead larvae were counted. The original number of herring larvae then was restored before a new experiment was started. Between experiments, the hyperiids were provided with food in order to reduce cannibalism.

RESULTS

Swimming and Feeding Behavior of
Hyperoche medusarum

Two modes of swimming were observed: 1) quick darting movements with the body kept in a horizontal position; and 2) slow hovering, in which the body was held in a vertical position, and the pleopods beat continuously. The latter mode of swimming was maintained for periods longer than 20 min, but the speed of swimming was slow (about 10 cm/min). It was only during swimming that *Hyperoche* would, by chance encounter, capture a herring larva. The amphipod usually grasped the tail but attacks at the head and the midportion of the larva also occurred. An attacked larva did not survive long. The larva attempted to shake the amphipod off for a few minutes, then sank to the bottom where it was eaten by the *Hyperoche*. Larvae were not always consumed. Frequently, amphipods clung to a larva for only a few seconds but the wound inflicted during this process inevitably lead to the death of the larva. Wounded larvae which were removed after termination of the experiment never survived for more than 4-5 h when kept in separate beakers.

Between swimming activities, the amphipods either remained on the bottom (probably an artifact due to the small size of the beakers—in large enough containers *Hyperoche* juveniles swam continuously (Westernhagen 1976)), or attached themselves with the posterior pereiopods to the nylon gauze provided in the beakers for this purpose and assumed a resting posture. This posture has been described for *Hyperia galba* by Bowman et al. (1963) and for *Hyperoche medusarum* by Evans and Sheader (1972). The latter authors defined the posture as an "inactive curled position head and urus directed away from the substrate it (the animal) sits on." Larvae that bumped into resting amphipods were not pursued or captured.

Predatory Efficiency of
Hyperoche medusarum

The results of all experiments were summarized and presented as the number of larvae attacked per hour at different predator and prey densities (Figure 1). The number of wounded and killed larvae was dependent on two factors, the density of the herring larvae and the density of hyperiids. With increasing numbers (predator or prey) larval mortality per hour increased, reaching a value of more than two larvae killed or wounded per hour at the 16 *Hyperoche* and 50 herring larvae combination.

The number of larvae attacked per unit time (1 h) depended to a great extend on the duration of the experiment (Figure 2). Experiments with short exposure times (2 h) yielded for all larvae and hyperiid combinations higher attack rates per hour than experiments lasting 4 or 8 h. The mean predatory efficiency of the hyperiids was affected also by their density in each beaker. The number of larvae attacked per unit time decreased as the density of the predators increased (Figure 3). It is for this reason that there are different values for the number of herring larvae attacked per hour by one hyperiid (Figure 4), (A) for the observation of one single hyperiid, and (B) for the calculated mean predation rate of a hyperiid from experiments with 1, 2, 4, 8, and 16 *Hyperoche*. Yet both curves show that an increase of a potential prey in a constant environment beyond a certain density
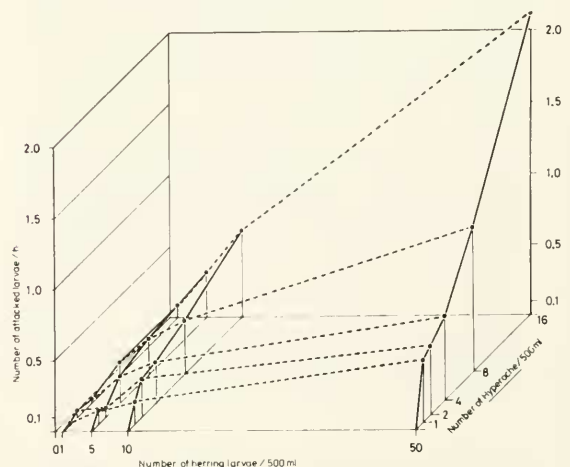

FIGURE 1.—Predatory efficiency of *Hyperoche medusarum* on yolk-sac larvae of *Clupea harengus pallasi* at different predator and prey densities. Water temperature: 9°C; total observation time: 111 h; observation periods: 20.
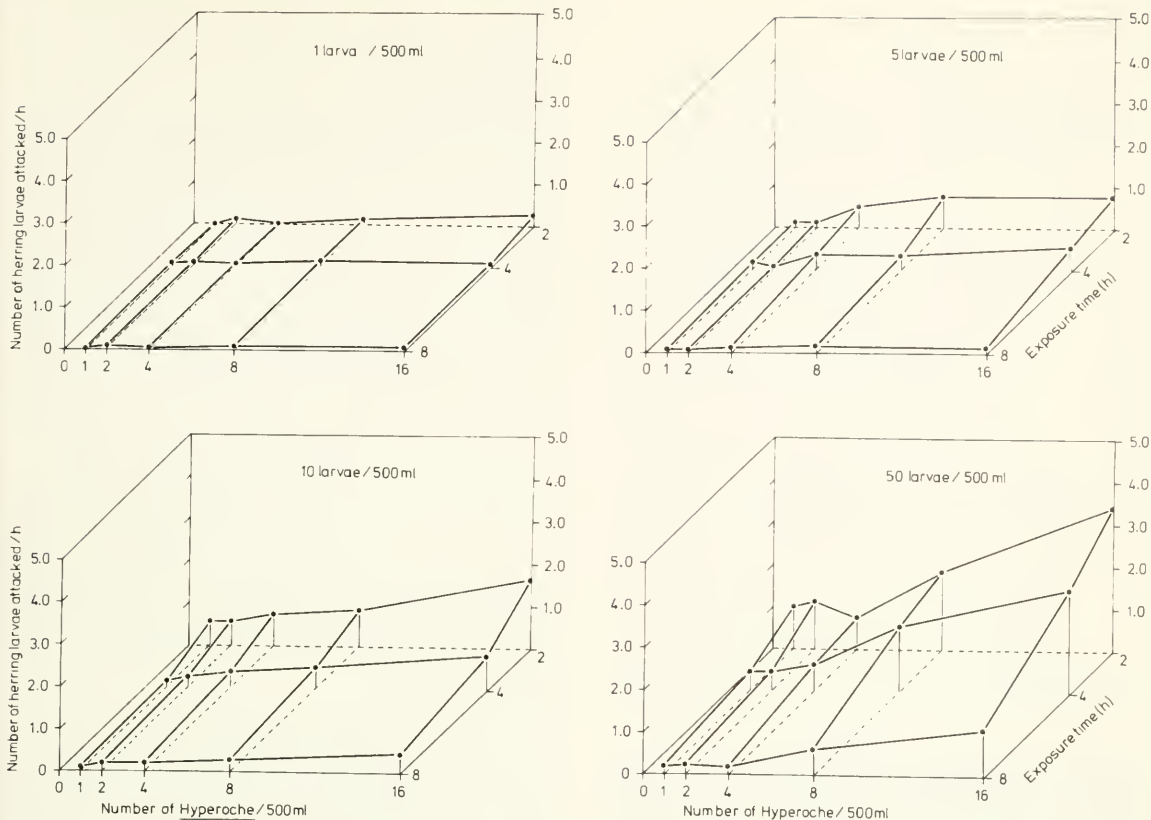
FIGURE 2.—Mean number of yolk-sac larvae of *Clupea harengus pallasi* attacked by *Hyperoche medusarum* after different exposure times. Water temperature 9°C.

does not necessarily lead to a corresponding increase in predation. At herring larvae densities of 5/500 ml and 10/500 ml, one individual hyperiid attacked 0.1 larvae/h and 0.16 larvae/h, respectively. At 50 larvae/500 ml the attack rate was 0.45 larvae/h. Assuming a linear increase in attack rate, we would have expected rates of 1.0 and 0.8 larvae/h.

Alterations in predation rates of *Hyperoche* were obtained when heterogenous prey was offered (25 herring larvae + 25 flatfish larvae), and Figure 3 shows that predation on larvae was remarkably reduced. Of the 0.07 larvae attacked per hour by one hyperiid, 0.055 (78%) were herring larvae and 0.015 (22%) flatfish larvae, thereby showing a pronounced preference for herring.

DISCUSSION

Figure 1 shows a clear, direct relationship between number of attacked larvae and both larval and hyperiid density. Increase in larval as well as predator density lead to increasing attack rates per hour. Because searching and contacting are random, this response was expected and has been described by Murdoch (1971) for predator-prey interaction. That relatively more larvae are attacked per hour during short exposure periods than during long ones (Figure 2) can be partially explained by a rapid thinning out effect on prey in confined containers, a problem discussed by Murdoch (1969) for the predation of *Thais* and *Acanthina* on *Mytilus* and *Balanus*. These data suggest that short observation periods are preferable in experiments of this type, a point frequently neglected in experiments with exposure times of 20 and more hours (Lillelund 1967; Lillelund and Lasker 1971; Theilacker and Lasker 1974; Ambler and Frost 1974), leading to an underestimate of the actual possible predation rate. An additional factor may be the degree of satiation, which could be shown for invertebrates to
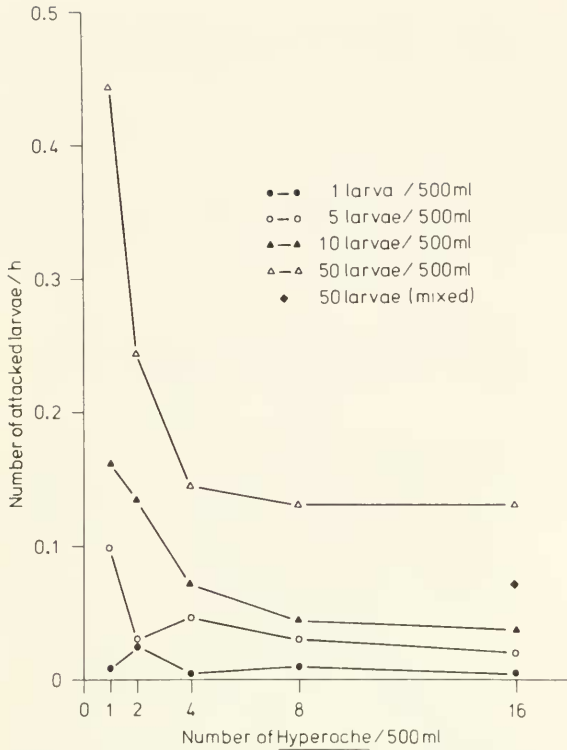
FIGURE 3. — Mean number of yolk-sac larvae of *Clupea harengus pallasi* attacked by *Hyperoche medusarum* during 1-h exposure time in an experimental volume of 500 ml at different larval concentrations. Water temperature 9°C. the "mixed" trial was provided with 25 herring and 25 flatfish larvae (11 replicates, 64 h total observation time).

FIGURE 4. — Mean number of yolk-sac larvae of *Clupea harengus pallasi* attacked per hour by one *Hyperoche* at different larval densities:
A. data of actual experiments with single hyperiids;
B. data obtained from mean values for experiments with 1, 2, 4, 8, and 16 hyperiids/500 ml.

reduce the rate of predation (Holling 1966; Brandl and Fernando 1974).

It became evident through the experiments that predation rate was also influenced by the number of predators present in an experimental beaker (Figure 3). Calculated mean individual predation rates in experiments using 50, 10, and 5 larvae decreased as the number of hyperiids in one container increased. Lillelund (1967) observed the same phenomenon in his experiment using cyclopids preying on larvae of *Osmerus eperlanus*, and Salt (1967) noted the same trend in experiments using the predatory protozoan *Woodruffia metabolica* preying on *Paramecium*. We consider this phenomenon an artifact caused by more than one predator feeding on the same prey, an event frequently observed at higher predator densities. This is unlikely to occur in the natural habitat, because a herring larva once killed by its predator which is still attached to it would sink down to the bottom out of the reach of the other *Hyperoche*.
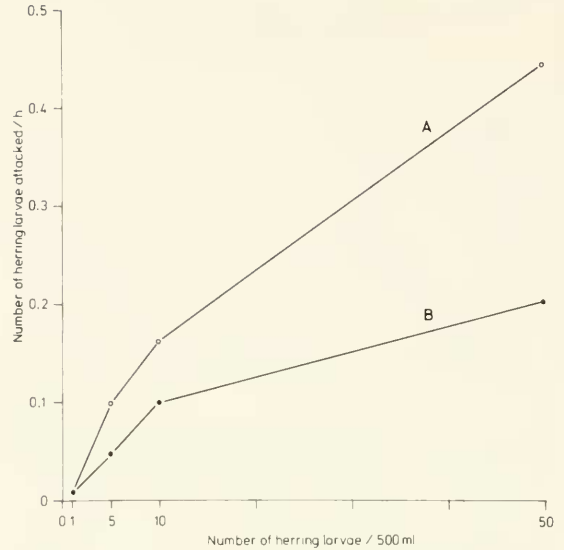
The number of herring larvae attacked did not increase proportionally with an increase of herring larvae available for the predators (Figure 4). This phenomenon has been termed "functional response" (type 2 response) by Holling (1966), and is believed to occur commonly in preying invertebrates. Similar responses are displayed by the house cricket, *Acheta domesticus* (Pimentel and Cranston 1960); *Podiscus maculiventris* (Morris 1963); *Acanthina* sp. (Murdock 1969); *Tortanus discaudatus* (Ambler and Frost 1974); and *Euphausia pacifica* (Theilacker and Lasker 1974). In a typical functional response curve, the number of prey eaten or attacked per predator increases to reach or approach a maximum at an asymptote (Murdoch 1971). Although the curves in Figure 4 do not yet approach an asymptote due to insufficient prey density, the trend towards a maximum attacking rate at a given prey density is noticeable.

Hyperoche medusarum exposed to two species of fish larvae clearly discriminated disproportionately between these two. In Figure 3, the total number of larvae attacked in trials providing alternate prey at equal densities is given as 0.7 individuals/h. Of these, 0.055 were herring larvae and 0.015 flatfish larvae. Discrimination between two prey species, which is likely to occur only in predators with searching and food selection

behavior (Murdoch and Marks 1973), might be either caused by different distribution of prey species (Oaten and Murdoch 1975), differences in palatibility (Holling 1965), avoidance behavior of the prey, or conditioning and/or training of the predator (Murdoch 1969; Oaten and Murdoch 1975) in cases of weak preferences.

Although generally *H. medusarum* was considered to lead a parasitic life on medusae (Sars 1895) such as *Cyanea capillata* (Bowman et al. 1963) or *Pleurobrachia pileus* (Evans and Sheader 1972), the results of our experiments show that even in the presence of alternate prey this amphipod displays considerable predation on herring larvae.

Unlike another carnivorous hyperiid, *Parathemisto gaudichaudi*, which hunts moving plankton visually (Sheader and Evans 1975), *H. medusarum* depends on random encounters with its prey. Many carnivorous copepods display the same behavior (Dziuban 1937; Fryer 1957; Lillelund 1967; Rosenthal 1972; Brandl and Fernando 1974; Ambler and Frost 1974). This mode of hunting requires a relatively high density of prey individuals which at times is provided by the enormous numbers of newly hatched herring larvae. During this investigation, herring larvae density during the day at the water surface was frequently above 2 larvae/100 cm² (direct observations). Simultaneous mass occurrences of *H. medusarum* suggest that the amphipods could possibly contribute considerably to herring larvae mortality, especially since conditioning to abundant prey organisms is comprehensible as could be shown by Sheader and Evans (1975) for *P. gaudichaudi* and its feeding on fish larvae. In fact stomach-content analyses of *H. medusarum* captured during this study period revealed that the amphipods had eaten considerable amounts of fish larvae (Westernhagen 1976).

ACKNOWLEDGMENTS

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